

Volumetric Comparisons in the Cerebellar Complex of Anthropoids, With Special Reference to Locomotor Types

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ABSTRACT Seven measurements in the cerebellar complex were completed on 45 individuals, including 26 species of anthropoids from Stephan's collection. These included 12 species of New World monkeys, 10 species of Old World monkeys, and *Hylobates*, *Gorilla*, *Pan*, and humans. The measurements were the volume of medial (fastigial) (CM), interpositus (globose and emboliform) (CI), and lateral (dentate) (CL) cerebellar nuclei, ventral pons (VPo), inferior olivary principal (OLIPr), and accessory (OLIAc) nuclei and vestibular nuclear complex (VES). The relative size of each nucleus was expressed in size indices based upon the allometric line obtained by the reduced major axis analysis. The indices of three cerebellar nuclei reflect the relative size of three longitudinal zones of the cerebellum. The cerebellar hemisphere-lateral zone is represented by the CL indices, the vermis-medialis zone by the CM indices, and the pars intermedialis-interpositus zone by the CI indices. The results show that the VPo and OLIPr indices are closely related to the CL indices. This lateral zone group of nuclei is the most progressively developed in humans, whereas the CM, CI, OLIAc, and VES are independent of the developmental trend manifest by the lateral zone group of nuclei. The indices are discussed in relation to the predominant locomotor pattern exhibited by a species.

The size indices of arboreal quadrupeds show a development of all nuclei in the cerebellar complex. This is interpreted as indicating that arboreal monkeys live in complicated, discontinuous, three-dimensional space and need exceptional cerebellar capacity for each pattern of locomotion and positional behavior. Progressive development of the lateral zone group of nuclei only compared to other nuclei was recognizable in humans. This development is considered to be related not to bipedalism, but to versatile and coordinated finger movement, resulting after bipedalism was established. This cerebellar reorganization is also a prerequisite (Leiner et al. [1993] *TINS* 16: 444–447) for the evolution of human language. The differences between size indices of the nuclei of *Macaca* (=pronograde primate) and *Ateles* (=antipronograde one) are compared in relation to their vertical climbing kinesiological data. *Am J Phys Anthropol* 103:173–183, 1997.

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Since Jansen and Brodal's study (1940) on the cerebellar cortico-nuclear projection, it has been generally accepted that the cerebellum has three principal components (or three

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longitudinal zones): the vermis-medialis nucleus component, the pars intermedialis-interpositus nucleus component, and the hemisphere-lateral nucleus component (Kuhlenbeck, 1975; Carpenter, 1976). Subsequently Voogd and Bigaré (1980) indicated further studies were needed to establish the significance of the zonal principle in the comparative anatomy of the cerebellum of higher primates. The medial zone is clearly related to muscle tonus, posture, and simple automatic movement. The lateral zone has a close relationship with the plan and program of fine, complex voluntary movement, and execution of locomotion is made possible by the control of the intermediate zone (Eccles, 1982; Ito, 1984). These functions of the cerebellum are also associated with the somatosensory system and the tracking of movements of targets in the environment (Paulin, 1993). Recent studies about the human cerebellum, focus on its non-motor function, such as cognitive and language functions (Petersen and Fiez, 1993; Leiner et al., 1993).

The size of the cerebellar nuclei is considered here to be an indication of variation in the three longitudinal zones among anthropoids. The structural organization of a nucleus is also closely related to its function and behavioral importance (Masterton et al., 1976; King, 1978). Accordingly, enlargement of a nucleus may reflect an increase in the number of neurons, in the size of the dendritic arborization and in the number of the synaptic terminals and other complexities in neuronal structures. Allometric comparisons of the size of a nucleus and body size or the rest of brain among various species in an order or family are therefore worth doing. The development of a nucleus and its adaptation to species-specific behavior such as animal locomotion described in this paper, can also be investigated through allometric comparisons.

Elsewhere one of us (S.M.) has discussed quantitative differences between some nuclei related to the cerebellar motor system in many species of anthropoids. In these studies, the least square regression line was used for each nucleus on body weight (Matano, 1986, for vestibular nuclear complex; Matano, 1992, for inferior olivary nuclei;

Matano et al., 1985a for ventral pons, 1985b for cerebellar nuclei). In all cases, Stephan's valuable collection for microscopy was employed.

For the classification of primate locomotion, we used the three principal categories of locomotion exhibited by living anthropoids, as given by Napier and Napier (1985): quadrupedalism, brachiation, and bipedalism. Among these primates, quadrupedalism includes four subtypes: branch running and walking, ground running and walking, New World semibrachiating and Old World semibrachiating. Brachiation is divided into two groups: (1) true brachiation in *Hylobates* and (2) modified brachiation (Orang type, Chimpanzee type, Gorilla type). Bipedal activity is manifest in standing, striding, and running.

In this paper, we summarize data on nucleus volumes that have already been reported: medial-fastigial (CM), interpositus-emboliform and globose (CI) and lateral-dentate (CL) cerebellar nuclei, ventral pons (VPo), inferior olivary principal (OLIPr) and accessory (OLIAc) nuclei, and vestibular nuclear complex (VES). We then analyse our findings, using newly obtained size indices. The latter are based upon the reduced major axis analysis line of each nucleus volume on body weight, and of each nucleus volume on the rest of medulla oblongata volume. Finally, we discuss the size indices in relation to anthropoid locomotor classification.

MATERIALS AND METHODS

Volumes of nuclei were measured in the brains of 45 individuals of 26 species of anthropoids from Stephan's collection. We follow Corbet and Hill (1991) in the assignment of anthropoid species names (Table 1). The collection of brains consists of the frontal and sagittal sections fixed in Bouin's fluid, embedded in paraffin, cut at 20–40 μm , and stained with cresyl violet for cells and by the Heidenhain-Woelche method for fibers. The details of this collection, and raw data on body weight and volume of the medulla oblongata of each species investigated are given by Stephan et al. (1981, 1988). The data on each nucleus volume and method of measurement has been previ-

TABLE 1. Name, number, body weight and locomotor type of species investigated¹

	n	Body weight (g)	Type
<i>Callithrix jacchus</i>	2	280	Small size AQ
<i>Cebuella pygmaea</i>	2	120	Small size AQ
<i>Saguinus midas</i>	2	340	Small size AQ
<i>Saguinus oedipus</i>	2	380	Small size AQ
<i>Cebus albifrons</i>	1	3,100	AQ
<i>Aotus trivirgatus</i>	2	830	AQ
<i>Callicebus moloch</i>	2	900	AQ
<i>Saimiri sciureus</i>	2	660	AQ
<i>Pithecia monachus</i>	2	1,500	AQ
<i>Alouatta seniculus</i>	2	6,400	SB
<i>Ateles geoffroyi</i>	1	8,000	SB
<i>Lagothrix lagothricha</i>	2	5,200	SB
<i>Macaca mulatta</i>	2	7,800	TQ
<i>Cercocebus albigena</i>	2	7,900	AQ
<i>Papio anubis</i>	2	25,000	TQ
<i>Cercopithecus ascanius</i>	2	3,400	AQ
<i>Cercopithecus mitis</i>	1	6,300	AQ
<i>Miopithecus talapoin</i>	2	1,200	AQ
<i>Erythrocebus patas</i>	2	7,800	TQ
<i>Colobus badius</i>	2	7,000	SB
<i>Pygathrix nemaeus</i>	1	7,500	SB
<i>Nasalis larvatus</i>	1	14,000	SB
<i>Hylobates lar</i>	1	5,700	TB
<i>Pan troglodytes</i>	1	46,000	MB
<i>Gorilla gorilla</i>	2	105,000	MB
<i>Homo sapiens</i>	2	65,000	SPB

¹ Locomotor type is based on Napier (1985). Values of body weights are from Stephan et al. (1981, 1988). AQ = arboreal quadrupedalism; MB = modified brachiation; SB = semibrachiation; SPB = specialized bipedalism; TB = true brachiation; TQ = terrestrial quadrupedalism.

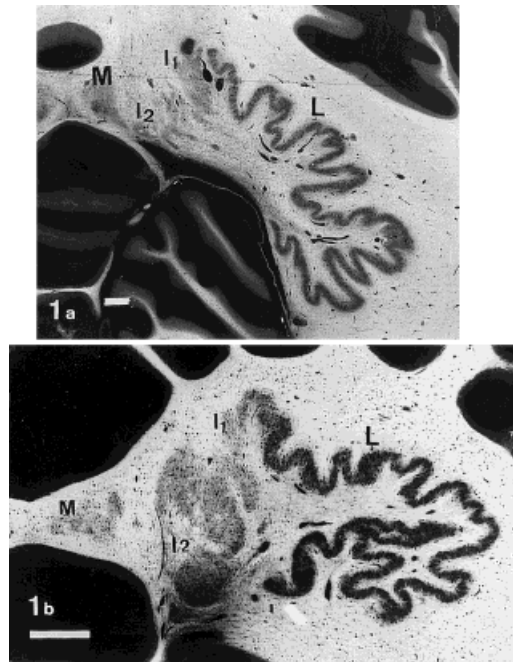


Fig. 1. The cerebellar nuclei, **a**: humans, **b**: *Hylobates*. M; the medial (fastigial) nucleus, I₁; the interpositus anterior (emboliformis) nucleus, I₂; the interpositus posterior (globosus) nucleus, L; the lateral (dentate) nucleus. Scale: 1 mm.

ously described (Matano, 1986, 1992; Matano et al., 1985a,b).

Figures 1 and 2 show some examples of three cerebellar nuclei of anthropoids investigated here. The volumes of globose and emboliform nuclei in human and apes were summed up as the volume of the interpositus nucleus (CI). In the monkeys the interpositus nucleus has two parts: (1) an anterior part located rostrally close to the lateral (dentate) nucleus that appears homologous to the emboliform nucleus, and (2) a posterior part located more medially that appears homologous to the globose nucleus (Carpenter, 1976).

The inferior olivary accessory nucleus (OLIAc) is divided into two nuclei (dorsal and medial), and the raw data have been reported (Matano, 1992). In this paper, OLIAc is the sum of two nuclei. Generally speaking, the OLIAc is phylogenetically old, whereas the OLIPr is recent (Kappers et al., 1960; Kuhlenbeck, 1975). The vestibular nuclear complex (VES) was divided into four

main nuclei. Several small groups of the vestibular complex described by Brodal and Pompeiano (1957) and Meessen and Olszewski (1949) were included in one of the four main nuclei (e.g., interstitial nucleus of vestibular nerve and group 1 in the lateral vestibular nucleus; group f, group x, and group z in the descending vestibular nucleus) (Matano, 1986). In this paper, the data on VES are the sum of these four main nuclei. Raw data obtained by Baron et al. (1988) are also used in this paper. For discussion of each of the nuclei, see Matano (1986).

The values of each nucleus volume were plotted on a double-logarithmic scale against body weight and against the rest of medulla oblongata volume, excluding each given nucleus, respectively. Thus, we tried to employ, as a base the lower brainstem, which is a fundamentally conservative part of brain structure among various primate species. Raw data of medulla oblongata volume collected by Stephan et al. (1981) include the pontile portion. The ventral pons, however,

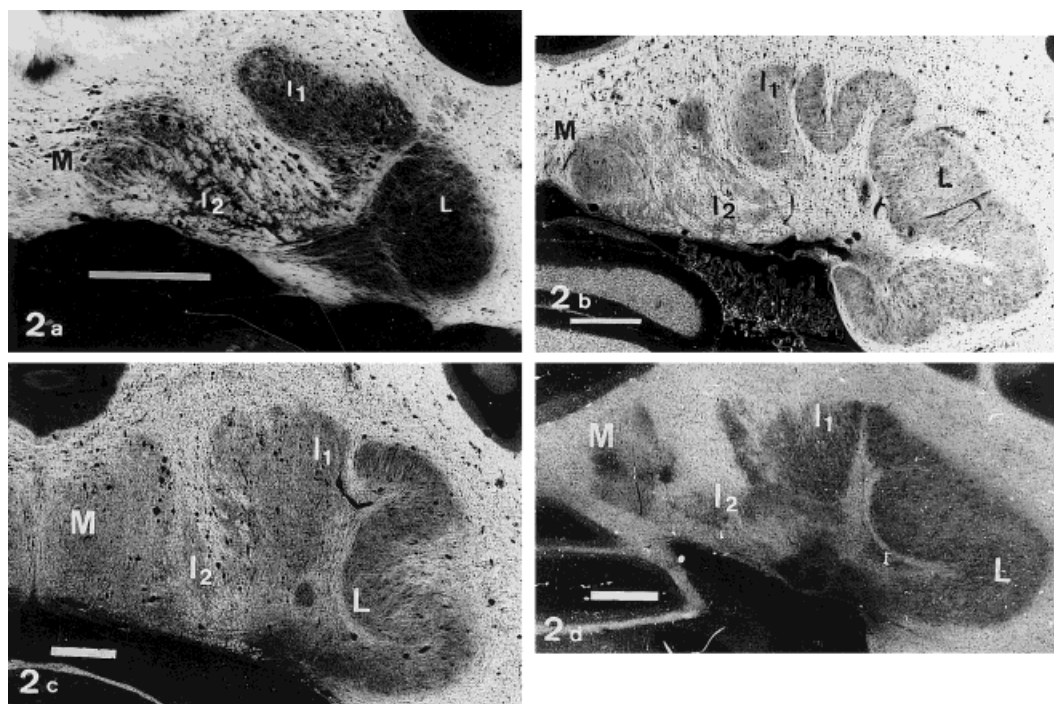


Fig. 2. The cerebellar nuclei of monkeys. **a:** *Callithrix*. **b:** *Lagothrix*. **c:** *Erythrocebus*. **d:** *Pygathrix*. For abbreviations see Figure 1.

extends often into the midbrain portion, especially in humans and great apes. Therefore, in the case of ventral pons (VPo), the medulla oblongata volume plus the midbrain were used for the rest of brain volume instead of the medulla oblongata volume alone. We could not obtain detailed raw data on the cerebellum from Stephan's collection, except for three cerebellar nuclei.

The equations of the allometric line were obtained by reduced major axis analysis (Harvey and Pagel, 1991) (Table 2). Examples of the line are shown in Figures 3 and 4. The values of each nucleus volume and the rest of medulla oblongata volume (R) are in mm³, and W is body weight in grams. Any value on these lines is considered to represent the average nucleus volume of a "typical" anthropoid. The distance from the reference line expresses the degree of deviation of the nucleus volume from those of a "typical" anthropoid. The reference line itself has, of course, a distance of 0, the antilog of which is 1 (i.e., size indices of the 26 anthropoids species is 1.0 on average

TABLE 2. Equations for each nucleus from reduced major axis analysis¹

Body weight (w)		
log CM(w)	= 0.64 log W - 0.791	(r ² = 0.874)
log CI(w)	= 0.64 log W - 0.699	(r ² = 0.874)
log CL(w)	= 0.64 log W - 0.442	(r ² = 0.949)
log VPo(w)	= 0.70 log W - 0.137	(r ² = 0.955)
log OLIPr(w)	= 0.67 log W - 1.343	(r ² = 0.912)
log OLIAc(w)	= 0.67 log W - 1.479	(r ² = 0.721)
log VES(w)	= 0.41 log W + 0.538	(r ² = 0.920)
Rest of medulla oblongata volume (r)		
log CM(r)	= 1.15 log R - 2.194	(r ² = 0.914)
log CI(r)	= 1.15 log R - 2.102	(r ² = 0.916)
log CL(r)	= 1.15 log R - 1.845	(r ² = 0.972)
log VPo(r)	= 1.58 log R - 2.606	(r ² = 0.962)
log OLIPr(r)	= 1.19 log R - 2.700	(r ² = 0.918)
log OLIAc(r)	= 1.19 log R - 2.837	(r ² = 0.762)
log VES(r)	= 0.72 log R - 0.282	(r ² = 0.964)

¹ CM, CI, CL: medial, interpositus and lateral cerebellar nuclei; OLIPr, OLIAc: inferior olivary principal and accessory nuclei; VES: vestibular nuclear complex; VPo: ventral pons.

in each nucleus, respectively) (Stephan, 1967).

Stephan's collection is the most extensive available, but the number of brains, which are sectioned serially, is limited. There are only two individuals per species and often there is only one individual (for example,

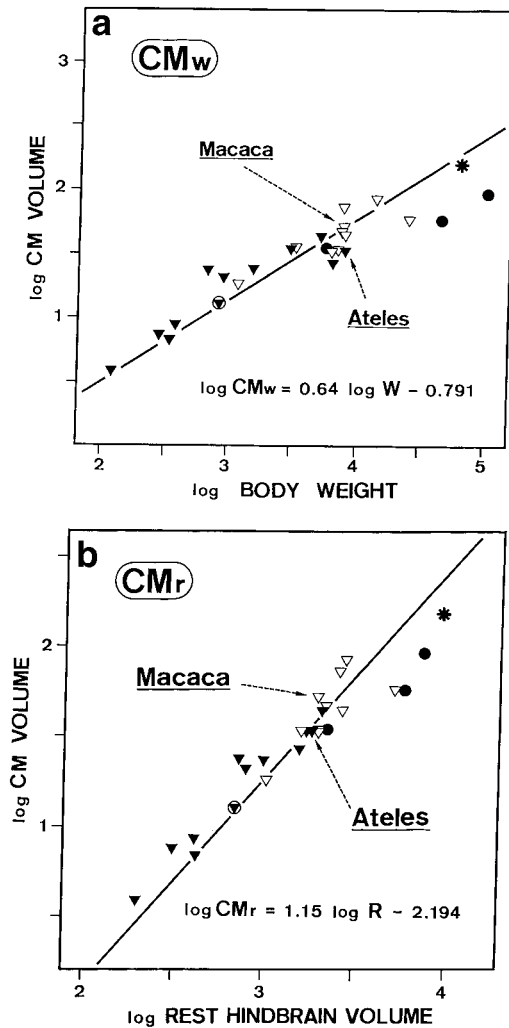


Fig. 3. **a,b:** The medial cerebellar nucleus (CM) volume (mm³) plotted against bodyweight (W) (g) (a, upper) and against the rest of medulla oblongata volume (R) (mm³) (b, bottom) on a double logarithmic scale. The reference line, which is determined by the reduced major axis analysis, is placed through the average of 26 species of anthropoids. ▼: New World monkeys; ▽: Old World monkeys; ●: Pongidae (including *Hylobates*); *: humans; ○: nocturnal.

Cebus, *Ateles*, *Nasalis*, etc.). Thus, the samples are too small to test for significance.

RESULTS AND DISCUSSION

Comparison of size indices

The size indices of each nucleus are provided for each species examined (Table 3). As we mentioned, statistical control is impos-

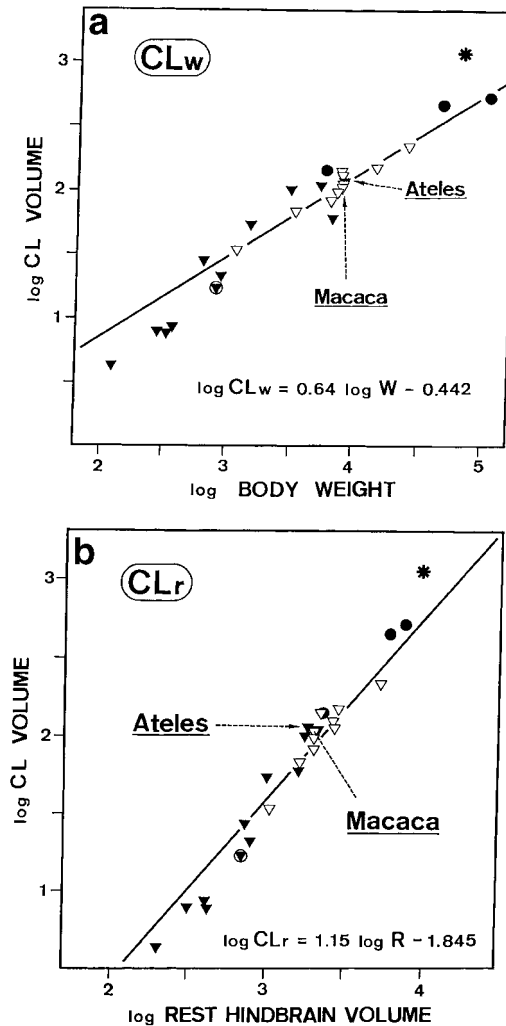


Fig. 4. **a,b:** The lateral cerebellar nucleus (CL) volume (mm³) plotted against body weight (a, upper) and against the rest of medulla oblongata volume (b, bottom) on a double logarithmic scale. See the explanation of Figure 3.

sible because of the small number of individuals sampled in each species. However, some trends are observable in our comparison of size indices.

Medial (fastigial) nucleus (CM). The average indices for Callitrichidae are high (1.2-w, 1.3-r), whereas humans and apes show very low values (Humans 0.80-w, 0.59-r, apes on average 0.53-w, 0.57-r), with particularly low values in the great apes. The highest indices are found in *Saimiri*. The

TABLE 3. Values for size indices of each nucleus in 26 species¹

Species	Nuclei													
	CM		CI		CL		VPo		OLIPr		OLIAc		VES	
	w ²	r ³	w	r	w	r	w	r	w	r	w	r	w	r
<i>Callithrix jacchus</i>	1.3	1.6	0.74	0.91	0.60	0.73	0.54	0.68	0.39	0.45	1.4	1.6	0.79	0.89
<i>Cebuella pygmaea</i>	1.1	1.4	0.75	0.91	0.56	0.68	0.44	0.60	0.64	0.76	1.7	2.1	0.90	1.0
<i>Saguinus midas</i>	1.0	1.0	0.83	0.83	0.51	0.51	0.55	0.57	0.50	0.46	1.5	1.4	0.88	0.86
<i>Saguinus oedipus</i>	1.2	1.3	0.80	0.89	0.54	0.60	0.57	0.66	0.49	0.52	1.3	1.4	0.89	0.96
<i>Cebus albifrons</i>	1.3	1.0	1.1	0.92	1.6	1.3	1.8	1.4	1.9	1.5	2.2	1.7	1.1	1.0
<i>Aotus trivirgatus</i>	1.3	1.1	0.77	0.79	0.64	0.66	0.71	0.85	0.54	0.52	1.1	1.0	0.96	0.96
<i>Callicebus moloch</i>	1.6	1.5	1.3	1.2	0.76	0.70	0.65	0.58	0.49	0.42	1.3	1.1	1.2	1.1
<i>Saimiri sciureus</i>	2.3	1.9	1.7	1.4	1.2	0.99	1.0	0.84	0.68	0.53	1.6	1.4	1.2	1.0
<i>Pithecia monachus</i>	1.4	1.3	1.5	1.4	1.4	1.3	0.90	0.79	1.2	1.1	1.4	1.2	1.1	1.0
<i>Alouatta seniculus</i>	0.62	0.89	0.49	0.70	0.61	0.87	0.61	0.84	1.1	1.5	1.1	1.5	0.61	0.77
<i>Ateles geoffroyi</i>	0.68	0.96	0.95	1.3	1.0	1.4	1.1	1.4	1.3	1.7	0.67	0.91	0.70	0.87
<i>Lagothrix lagotricha</i>	1.1	1.0	1.3	1.0	1.3	1.1	1.3	0.90	1.5	1.3	0.89	0.75	0.90	0.84
<i>Macaca mulatta</i>	1.1	1.3	1.2	1.5	0.96	1.2	0.87	0.96	1.4	1.7	1.2	1.4	1.1	1.3
<i>Cercocebus albigena</i>	0.89	0.79	1.2	1.1	1.0	0.91	1.2	0.85	1.1	0.92	1.1	0.94	1.2	1.2
<i>Papio anubis</i>	0.56	0.48	0.76	0.66	0.93	0.81	1.3	0.99	0.67	0.53	0.86	0.69	1.0	0.91
<i>Cercopithecus ascanius</i>	1.2	1.1	1.1	1.1	1.0	0.98	1.3	1.0	1.4	1.3	1.4	1.3	1.2	1.1
<i>Cercopithecus mitis</i>	0.78	0.86	1.0	1.1	0.84	0.93	0.81	0.73	0.83	0.86	0.93	0.98	1.1	1.2
<i>Miopithecus talapoin</i>	1.2	1.0	1.4	1.1	1.0	0.82	1.4	0.97	1.8	1.4	1.9	1.5	1.4	1.2
<i>Erythrocebus patas</i>	1.5	1.4	1.5	1.4	1.1	1.1	1.1	0.86	0.80	0.69	0.94	0.81	1.2	1.2
<i>Colobus badius</i>	0.69	0.85	1.0	1.2	0.94	1.1	0.94	0.99	1.1	1.2	0.79	0.87	0.90	0.99
<i>Pygathrix nemaeus</i>	0.98	1.1	1.3	1.4	1.3	1.4	0.98	1.0	1.2	1.2	0.89	0.92	0.87	0.92
<i>Nasalis larvatus</i>	1.2	1.4	1.2	1.3	0.92	1.1	0.87	0.97	1.2	1.4	0.88	0.98	0.99	1.1
<i>Hylobates lar</i>	0.86	0.77	1.3	1.2	1.5	1.4	2.0	2.0	3.2	2.7	1.8	1.5	0.99	0.93
<i>Pan troglodytes</i>	0.37	0.43	0.45	0.52	1.3	1.5	1.6	1.9	1.1	1.1	0.13	0.15	0.79	0.87
<i>Gorilla gorilla</i>	0.35	0.51	0.34	0.50	0.90	1.3	1.2	2.1	0.90	1.2	0.24	0.33	0.63	0.81
<i>Homo sapiens</i>	0.80	0.59	0.79	0.63	2.7	2.1	3.3	3.4	2.5	1.8	0.41	0.31	1.0	0.92

¹ See Table 2 for definitions of acronyms.² w = values obtained from equation for body weight.³ r = values obtained from the equation for the rest of the medulla oblongata volume.

range of variation in indices for Cebinae overlaps with that for Old World monkeys. However, the average indices for the former (1.3-w, 1.2-r) are clearly higher than those for the latter (1.0-w, 1.0-r).

Interpositus (globose and emboliform) nucleus (CI). Values of Callitrichidae are inferior to that of average (1.0). Humans and great apes have still lower values. *Hylobates*' indices (1.3-w, 1.2-r) fall between the range of variation among Old World monkeys. The values of Cebinae show a considerable overlap with those of Old World monkeys. Among them, *Alouatta* and *Papio* occupy the lowest position in index values, respectively.

Lateral (dentate) nucleus (CL). The distinctly lowest average is found for Callitrichidae (0.55-w, 0.63-r) and the clearly highest for humans (2.7-w, 2.1-r). The values for humans surpass the range of variation for non-human simians (0.51 ~ 1.6-w, 0.51 ~ 1.5-r). Apes' indices are clearly higher than the average values among Old World mon-

keys. The low values of size indices for body weight in *Gorilla* (0.90-w) may be due to excess body weight. The range of variation of indices for Cebinae overlaps fully with that for Old World monkeys.

Ventral pons (VPo). Very low values are recognized in Callitrichidae on average (0.65-w, 0.63-r). The highest indices by far are found in humans. The values for apes clearly occupy a high position compared with those for Old World monkeys. Among them, relatively lower indices for *Gorilla* are seen in values for "w" (1.2-w). This may be due to excess body weight in this species. Among monkeys, *Cebus* shows very high index values. As a result, the trend in variation of size indices for VPo is considered to be similar to that for CL.

Inferior olivary principal nucleus (OLIPr). Remarkably low values are found in Callitrichidae on average (0.51-w, 0.55-r). In contrast, *Hylobates* and humans occupy the highest position among the OLIPr indices.

TABLE 4. Values for correlation coefficients between indices of each nucleus¹

(r) \ (w)	CM	CI	CL	VPo	OLiPr	OLiAc	VES
CM	—	0.72	-0.045	-0.23	-0.20	0.59	0.59
CI	0.61	—	0.23	0.022	0.22	0.46	0.74
CL	-0.41	0.019	—	0.92	0.74	-0.18	0.19
VPo	-0.59	-0.39	0.85	—	0.79	-0.20	0.16
OLiPr	-0.38	0.14	0.68	0.60	—	0.13	0.15
OLiAc	0.59	0.3	-0.53	-0.54	-0.040	—	0.49
VES	0.33	0.59	-0.14	-0.29	-0.044	0.19	—

¹ Based on 45 individuals from 26 species. The numbers are too small for the significance of the correlation. For the meaning of acronyms, see Table 2. The underscored values are referred to in the text.

The values for great apes are relatively high, but are within the range of variation of indices for monkeys. Among monkeys, *Aotus*, *Callicebus*, *Saimiri*, and *Papio* show very low indices, resembling those of Callitrichidae.

Inferior olivary accessory nucleus (OLiAc). Callitrichidae show the highest level in size indices (1.5-w, 1.6-r on average). The values for humans and great apes are extremely low. The range of variation of the indices for Old World monkeys overlaps with those for Cebinae.

Vestibular nuclear complex (VES). The range of variation in size indices for VES is relatively narrow in comparison with those for other nuclei mentioned above. Callitrichidae occupy a relatively low position (0.87-w, 0.93-r on average). Among Old World monkeys, Cercopithecinae's indices are somewhat higher than those of Colobinae.

Clearly, CL, VPo, and OLiPr reveal a remarkable development in apes and humans, whereas development in Callitrichidae is poor. The values of the coefficients in the size indices are shown in Table 4. The statistical significance of the values is not given, because of small sample sizes, but a relatively high correlation with the CL is recognized for VPo (0.92-w, 0.85-r) and OLiPr (0.74-w, 0.68-r). The correlation between VPo and OLiPr is also high (0.79-w, 0.60-r). These three nuclei play an important role in the neural circuit related to the function of the hemisphere-lateralis zone, which is concerned with planning and programming of fine complex voluntary movements (Eccles, 1982; Ito, 1984). For this reason, we call CL, VPo, and OLiPr the lateral zone group of nuclei. CI, however, does not seem to have a definite trend in its development.

In contrast, CM for the vermis-medialis zone, which is concerned with posture and simple automatic movement (Eccles, 1982; Ito, 1984), shows the highest development in Callitrichidae, and very poor development in great apes and humans. The development trend for OLiAc is similar to that for CM. The development for VES is relatively high in Cercopithecinae in comparison with those in other groups that we investigated.

Relationship between the size indices of each nucleus and anthropoid locomotor type

Among arboreal quadrupeds, the Callitrichidae differ from the Cebinae and Cercopithecinae in their pattern of locomotion in part because the former are very small in body size in relation to the latter (about 1/10 in the average of bodyweight). Napier and Napier (1985) said that the term semibrachiator has not proved particularly apposite in New World and Old World monkeys. Among the New World semibrachiators, *Alouatta* is more a quadrupedal climber rather than a brachiator (Grand, 1968). Therefore, we excluded *Alouatta* from our semibrachiator results. The ground running and walking anthropoids include *Macaca*, *Papio*, and *Patas*. Among them, *Macaca* exhibits perhaps, more of a semiterrestrial locomotor pattern than a terrestrial one.

No locomotor type is dependent on control by only the cerebellar hemisphere-lateralis zone or the vermis-medialis one. However, many locomotion patterns observed under normal circumstances can be interpreted to be under the predominant control of either the lateral zone or the medial one.

In Table 5, the size indices (w, r) are given according to the classification of the given

TABLE 5. Size indices of each nucleus on average viewed from various locomotor types¹

	n ²	CM		CI		CL		VPo		OLiPr		OLiAc		VES	
		w ³	r ⁴	w	r	w	r	w	r	w	r	w	r	w	r
Small size AQ	4	1.2	1.3	0.78	0.89	0.55	0.63	0.53	0.63	0.51	0.55	1.5	1.6	0.87	0.93
AQ	9	1.3	1.2	1.2	1.1	1.0	0.95	1.1	0.89	1.1	0.95	1.4	1.2	1.2	1.1
SB	5	0.93	1.1	1.2	1.3	1.1	1.2	1.0	0.84	1.3	1.4	0.82	0.88	0.87	0.94
TB	1	0.86	0.77	1.3	1.2	1.5	1.4	2.0	2.0	3.2	2.7	1.8	1.5	0.99	0.93
MB	2	0.36	0.47	0.40	0.51	1.1	1.4	1.4	2.0	1.0	1.2	0.19	0.24	0.71	0.84
SBP	1	0.80	0.59	0.79	0.63	2.7	2.1	3.3	3.4	2.5	1.8	0.41	0.31	1.0	0.92

¹ For the meaning of acronyms, see Tables 1 and 2.² n = number.³ w = values obtained from the equation for body weight.⁴ r = values obtained from the equation for the rest of the medulla oblongata volume.

species' main locomotor pattern. With regard to knuckle walking and modified brachiating in great African apes, the development of CM, OLiAc, and VES is extremely poor and occupies the lowest position among all of the anthropoids we investigated (Table 5). This is also true with respect to the development of CI. On the other hand, CL, VPo, and OLiPr (the lateral zone group of nuclei) show a pronounced development. This trend in animals with modified brachiation, that is, lower values of CM, OLiAc, VES, and CI vs. higher values of the lateral zone group of nuclei, is similar to that seen with bipedalism (Table 5). However, each value of the size indices tends to be lower in modified brachiators than that in the specialized bipeds. In Figure 5, the typical pattern of variation for three cerebellar nuclei indices (r) is reflected in the locomotor types of arboreal quadrupeds, true brachiation, modified brachiation, and specialized bipeds.

Among arboreal quadrupeds, the size indices of the lateral zone group of nuclei are clearly lower in Callitrichidae (small in body size) than in other arboreal quadrupeds. The lower values for Callitrichidae show that the ability for fine, complex voluntary movement is inferior in these animals in comparison with other simians.

Among arboreal quadrupeds, a balance is maintained between the size indices of the lateral zone group of nuclei with CI and those of CM, OLiAc, VES. This evidence indicates that arboreal monkeys usually live in complicated, discontinuous, three-dimensional space, and need exceptional capacity in each pattern of locomotion and positional behavior (Table 5, Fig. 5).

Some comments are required regarding Napier and Napier's terrestrial quadrupedal locomotor type. We investigated three species: *Papio anubis*, *Macaca mulatta*, and *Erythrocebus patas* (Tables 1 and 3). In the values obtained for CM, CI, OLiAc, and VES, *Papio* occupies a markedly lower position than *Macaca* and *Patas*. The size indices of each nucleus reach a high level in *Macaca*. This trend resembles what occurs

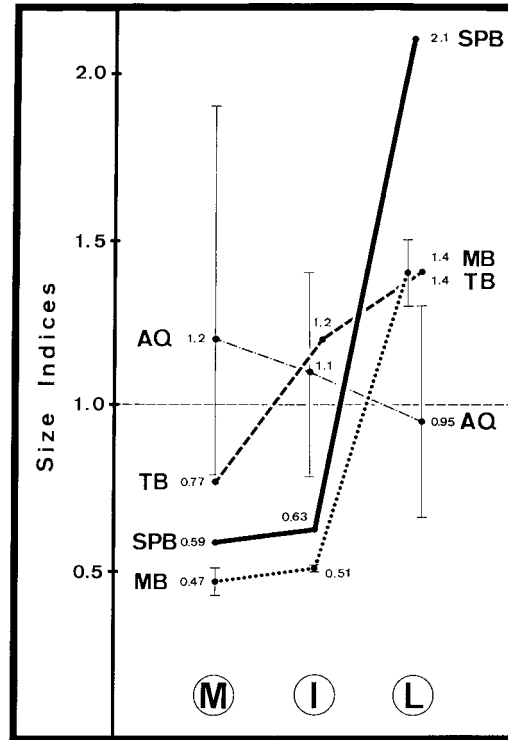


Fig. 5. Size indices for the rest of medulla oblongata volume (r) of the medial (M), interpositus (I), and the lateral (L) cerebellar nuclei in various locomotor types of anthropoids. AQ: arboreal quadrupeds (N = 9), TB: true brachiator (*Hyllobates*), MB: modified brachiators (N = 2), SPB: specialized bipedalism.

in arboreal quadrupeds. *Macaca* exhibits semiterrestrial locomotion rather than a terrestrial one. The indices of *Erythrocebus* are also large. As well known, *Erythrocebus* is an extremely fast runner with a cheetah-like gait (Napier and Napier, 1985). Therefore, Napier and Napier's terrestrial quadrupedal classification comprises different locomotor patterns when viewed from the development of the cerebellar motor system.

Napier and Napier classified semibrachiators in the quadruped category. The range of variation for the nucleus indices in semibrachiators shows a considerable overlap with those in arboreal quadrupeds, though semibrachiators' indices are relatively higher in OLIPr and lower in OLIAc on average (Table 5). The classification of semibrachiation is considered to not be apposite (Napier and Napier, 1985). Viewed from the development of the cerebellar motor system, it is impossible to distinguish clearly between semibrachiation and arboreal quadrupedalism. Further detailed analysis of this issue is warranted.

Special attention needs also to focus on the size indices in *Ateles* (=antipronograde primates) and *Macaca* (=pronograde one). Table 3 and Figures 3 and 4 show that values of size indices of CM, OLIAc, and VES in *Ateles* are relatively lower than those in the lateral zone group of nuclei with the CI. However, in *Macaca* we observed a high position, and maintenance of balance in all nuclei investigated. Nucleus size indices in *Ateles* are somewhat similar to those of African great apes, but those in *Macaca* resemble those of arboreal quadrupeds. This difference between *Ateles* and *Macaca* is thought to reflect bipedal walking (Yamazaki, 1985) and vertical climbing (Hirasaki et al., 1992, 1993) as shown in kinesiological studies.

Yamazaki first noted the potential ability for bipedal walking by *Macaca*, *Ateles*, *Hylobates*, and Chimpanzee. He estimated the internal force of the hip and knee joints, and the energy cost for the walking in his experiments. Then, he calculated similarity indices of the walking pattern obtained from kinesiological data with computer-simulated values. The similarity indices were utilized for the calculation of potential abil-

ity for bipedal walking. If the values of this potential ability are 100 for humans and 0 for *Macaca*, those of *Hylobates*, chimpanzee, and *Ateles* were estimated as 40, 28, and 11, respectively. Therefore, the potential abilities of *Ateles* (antipronograde monkey advocated by Stern, 1975) are closer to those of great apes and humans than to those of *Macaca* (pronograde monkey).

Hirasaki et al. (1992, 1993) showed in their vertical climbing experiment that (1) *Ateles* extends its joints more than does *Macaca*, (2) the hindlimb of *Ateles* contributes more to climbing than does that of *Macaca*, and (3) the angular displacement pattern and the locus of the force application point indicate "push-off propulsion" by the ankle joint of *Ateles*. These differences between *Ateles* and *Macaca* suggest that vertical climbing exhibited by *Ateles* may be closer to being a preadaptation for bipedal walking than that shown by *Macaca*. Accordingly, these results also support the "vertical climbing theory" for the phylogeny of bipedalism (Prost, 1980; Fleagle et al., 1981).

Finally, we note the importance of true brachiating. *Hylobates* has reached a high development of all nuclei in the cerebellar complex. Especially, the CM, OLIAc, and CI indices are far better developed in *Hylobates* than in modified brachiators (Table 5, Fig. 5). Unfortunately, for reasons stated previously, it is impossible to judge this observation statistically. Nevertheless, the locomotion of *Hylobates* is considered to be in accordance with those higher indices of the progressive cerebellar motor system. This species is extremely active and agile, and shows effortless ease in "flying" through the trees.

Yamazaki's (1985) computer simulations also showed that *Hylobates*' bipedal walking is closest to that exhibited by humans. However, the nucleus index values are clearly different between both species. Table 5 and Figure 5 show that size indices of CL and VPo in the lateral zone group of nuclei in humans are extremely high, whereas those of CM and OLIAc are markedly low. This suggests that the eminent progressive development of only the lateral zone group of nuclei in humans depends not upon bipedal locomotion, but on skillful voluntary finger

movement resulting from emancipation of the upper limb. Further evidence is provided by the size indices of the interpositus (globose and emboliform) nucleus, which is concerned with execution of locomotion (Eccles, 1982; Udo et al., 1981). These are clearly lower in humans than in *Hylobates* (Table 5, and Fig. 5).

Thus, only the extreme progressive development of the lateral zone group of nuclei (CL, VPo, OLIPr), which is characteristic of the cerebellar complex in humans, connects with the evolution of the supplementary motor cortex in the frontal lobe via the thalamus (Rouiller et al., 1994). This reorganization of the cerebro-cerebellar circuit presumably occurred with the appearance of *Homo habilis*, because specialized bipedal walking, which constitutes almost the same pattern as seen in living humans, was established in *Homo habilis* (Napier, 1970; Pilbeam, 1988; Tobias, 1971, 1991).

Our proposal for cerebellar reorganization during hominid evolution is in accordance with recent data from neuroimaging and neurobehavioral studies, which were obtained from normal adult cerebella and patients with defective cerebella (Petersen and Fiez, 1993; Leiner et al., 1993). These data show that the human cerebellum is involved in cognitive and language functions. This functional expansion is considered to be a consequence of cerebellar reorganization during hominid evolution, and this could have been a prerequisite for the evolution of human language (Leiner et al., 1993).

CONCLUSION

A striking reorganization of the cerebellar motor system in primate brains is associated with a change in ecological niche: from the stable ground-living habitat, to more diverse, complicated, discontinuous, three-dimensional arboreal life. Arboreal quadrupeds have a development of all nuclei in the cerebellar complex. They need exceptional capacity in each pattern of locomotion and positional behavior. The reorganization of the cerebellar motor system for bipedalism in human locomotion after the return to the ground may have evolved relatively easily by a little modification of this excellent system that had evolved in arboreal life. The

eminent progressive development of only the lateral zone group of nuclei in the human cerebellum is considered to have developed not for bipedalism, but for skillful voluntary finger movement resulting from emancipation of the upper limb. Furthermore, this reorganization of human cerebellum could have been a prerequisite for the evolution of human language (Leiner et al., 1993).

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